# Banding pattern comparisons between Akodon iniscatus, and Akodon puer (Rodentia, Cricetidae) 

By Maria A. Barros, Rosa C. Liascovich, L. Gonzalez, Martha S. Lizarralde, and O. A. Reig

GIBE, Dpto. de Cs. Biológicas, FCEyN, Universidad de Buenos Aires, Argentina, Instituto de Evolución y Ecologia, Universidad Austral de Chile, Valdivia, Chile, and Centro Austral de Investigaciones Científicas, CONICET, Ushuaia, Argentina

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#### Abstract

Described the chromosomes of Akodon iniscatus ( $2 \mathrm{n}=33-34, \mathrm{FN}=42$ ) and compared with the karyotypes of $A$. $\operatorname{puer}(2 \mathrm{n}=34, \mathrm{FN}=40)$. 37 specimens of $A$. iniscatus and 11 of $A$. puer were studied on their $\mathrm{C}, \mathrm{G}$ and fluorescent ( Q and CMA) banding patterns. Whole chromosomes and chromosome arms were shared between both species, 38 arms showed the same G-banding pattern in both species. A. iniscatus contains mainly wide-spread centromeric heterochromatin that is absent in A. puer and rare in other akodonts. Chromomycin banding revealed that centromeric heterocromatin was homogeneous and GC poor in all chromosomes, whereas the telomeric heterochromatin was GC rich. The present results support the hypothesis of close relationship between A. iniscatus and A. puer and that the former probably derived from an Akodon stock originally differentiated in the low-lands of northeastern Argentina. Therefore, A. iniscatus is related with the varying $2 \mathrm{n}=40$ akodont chromosome group.


## Introduction

Akodon is a highly speciose genus of South American cricetids that is the most widely and better known of the genera of sigmodontine mice in its cytogenetics. Of the 38 recognized species of Akodon (Reig 1987), 29 are known in their karyotype and 17 have also been analysed in their banding patterns (Bianchi and Merani 1980; Bianchi and Merani 1984; Bianchi et al. 1976; Gallardo 1982; Lobato et al. 1982; Rodriguez et al. 1983; Vitullo et al. 1986; Yonenaga et al. 1975, 1976; Yonenaga-Yassuda 1979).

Akodon iniscatus Thomas is one of the few species of the genus for which the chromosomal complement has not been described. Several specimens from Collón Curá, Neuquén Province, Argentina were karyotyped some time ago by two of the present authors (O. A. R. and L. G.), but these determinations remained unpublished. More recently, $A$. iniscatus was found to be the most common cricetid in the coastal region of Chubut Province, Argentina where its presence had not been reported previously. A. iniscatus karyotype was very similar to that of Akodon puer Thomas, (Barquez et al. 1980; Kajon et al. 1984; Vitullo et al. 1986). Cytogenetic results on A. iniscatus and their comparison with new results from specimens of $A$. puer are presented here.

## Material and methods

Cytogenetic analysis was performed on 37 specimens of $A$. iniscatus from Chubut and Neuquén Provinces and on 11 specimens of $A$. puer from Jujuy Province, Argentina. Localities for A. iniscatus were: 5 km S Pto. Madryn, Chubut ( 13 females and 18 males); Punta Lomas, 20 km S Pto. Madryn, Chubut ( 2 males), and Collón Curá, Neuquén ( 2 females and 2 males). A. puer was collected from León, Jujuy ( 7 females and 4 males). These specimens are deposited as skin and skull museum specimens in the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia" of Mar del Plata,

Argentina (MMP), and in the Collection of Mammals of the Centro Nacional Patagónico (CNP), in Puerto Madryn, Argentina.

Additional specimens have been studied for taxonomic comparisons and identification. These include the type specimen of $A$. nucus at the British Museum of Natural History (BMNH 26.10.1142, male from Chos Malal, Neuquén), the type of $A$. iniscatus (BMNH 3.7.9.64, female from Valle del Lago Blanco, Chubut), a topotypical series of $A$. iniscatus, and 4 specimens from 20 km S of Leleque, Chushamen, Chubut.

For taxonomic studies, cranial and molar tooth morphology were examined with a Wild M-5 stereomicroscope. Skull and teeth were measured with a digital caliper and/or with an eye-piece reticule of the stereomicroscope to the nearest 0.1 mm following standard conventions.

Metaphase chromosome preparations were obtained from bone marrow (Barros and Patton 1985) of animals injected with yeast 24 hs prior to sacrifice (Lee and Elder 1980). C-bands were obtained following the procedure described in Barros and Patton (1985). Seabright's (1971) procedure was followed for G-bands. Chromomycin $A_{3} /$ methyl green (CMA) bands were done according to HACK and LAwCE (1980). Quinacrine/actinomycin D (Q) banding was done according to Hack and Lawce (1980). All fluorescent bands were photographed with Kodak Tri-X film exposed at ASA 800.

Diploid number and chromosome morphology were determined for all specimens, chromosomes were classified according to Levan et al. (1964). Reig and Kiblisky's (1969) size proposal convention was followed. Fundamental number is defined as the number of autosomal arms.

## Results

## Taxonomy

The type specimens of A. iniscatus Thomas, 1919 and of A. nucus Thomas, 1926 were found in Valle del Lago Blanco, SW of Chubut and Chos Malal, N of Neuquén, respectively. The two localities are separated by nearly 935 km in the mountainous region of the southern Andean slopes of Argentina (Fig. 1). The type specimens show that the two taxa are very similar in external, skull and tooth features, though they differ markedly in size, $A$. nucus being noticeably larger than $A$. iniscatus. $A$. nисиs also differs from $A$. iniscatus in having nasals longer than frontals, parietals comparatively longer, the anterior border of the zygomatic plate in an upward position, and the M3 relatively smaller (Fig. 2).

Judging from the holotypes and additional topotypical or referred specimens in the British Museum of Natural History, the differences found seem to justify full species


Fig. 1. Map showing localities of $A$. iniscatus and A. nucus. 1. Chos Malal (type locality for $A$. iniscatus); 2. Collón Curá; 3. El Maitén; 4. Leleque; 5. Lago Blanco (Type locality for A. nucus); 6. Puerto Madryn
distinction, as proposed by one of us (Reig 1987). However, Cabrera (1961) considered that $A$. nucus is merely a subspecies of $A$. iniscatus, a course implicitly followed by Honacki et al. (1982), who did not list $A$. nucus as a separate species.

Our specimens from Collón Curá, a locality for which Thomas (1927) cited A. nuсиs, are fairly similar to the holotype of this species, and share all its distinctive characters. Our small available series from Leleque, which comes from 42 km S of Maitén, the type locality of the local form $A$. iniscatus collinus Thomas, 1919, is almost undistinguishable from $A$. iniscatus, thus confirming the distinction of the two (Table 1).

However, our sample from localities near Puerto Madryn, a region where no Akodon of this group has been found previously, is quite intermediate between $A$. nucus and $A$. iniscatus in size and morphology (Table 1). Additionally, the karyotype of specimens from these localities are similar to those from Collón Curá reported in this paper. Thus, the intermediacy of the Puerto Madryn Akodon as regards typical A. iniscatus and A. nucus, sheds doubts on the species status of $A$. nucus. We are probably dealing with a geographically variable group of populations which are better considered, at the present state of knowledge, as a single polytypic species. It would support Cabrera's proposal of treating $A$. nucus as a subspecies of $A$. iniscatus. However, this issue is a tentative one, and must be tested by further morphological and cytogenetic studies. But at present, we prefer to allocate provisionally all our chromosomally studied specimens to Akodon iniscatus without further refinement.


Fig. 2. Skull in lateral, dorsal, and ventral views of the holotypes of $A$. iniscatus and $A$. nucus

Table 1. Measurements (mm) of A. iniscatus (AI) and A. nucus (AN) holotypes, and samples from Leleque, Puerto Madryn, and Collón Curá. N: sample size; X: mean; SD: standard deviation

| Variable | $\begin{gathered} \text { AI } \\ \text { Type } \end{gathered}$ | $\begin{gathered} \text { AN } \\ \text { Type } \end{gathered}$ | Leleque sample |  |  | PTO. Madryn sample |  |  | Collón Curá sample |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | N | X | SD | N | X | SD | N | X | SD |
| Total length | 145.0 | 181.0 | 4 | 140.0 | 6.4 | 11 | 153.0 | 8.3 | 4 | 173.0 | 8.6 |
| Tail length | 53.0 | 77.0 |  | 55.8 | 2.2 | 11 | 60.2 | 6.0 | 4 | 65.9 | 3.9 |
| Hind foot | 19.0 | 23.0 | 4 | 18.9 | 0.6 | 12 | 20.6 | 0.9 | 4 | 22.6 | 1.0 |
| Ear | 11.0 | 14.0 | 4 | 11.8 | 0.2 | 12 | 12.5 | 0.7 | 4 | 12.8 | 1.5 |
| Skull total length | 23.7 | 26.8 | 4 | 23.0 | 0.6 | 13 | 24.5 | 0.9 | 4 | 25.8 | 0.2 |
| Condylo basal | 21.7 | 25.2 | 4 | 20.8 | 0.5 | 13 | 22.6 | 0.9 | 4 | 24.0 | 0.1 |
| I-M3 | 11.1 | 12.4 | 4 | 10.5 | 0.3 | 13 | 11.1 | 0.4 | 4 | 12.0 | 0.3 |
| Diastema | 5.6 | 6.7 | 4 | 5.5 | 0.3 | 13 | 6.0 | 0.3 | 4 | 6.4 | 0.2 |
| Zygomatic breadth | 12.4 | 14.7 | 4 | 11.7 | 0.3 | 13 | 12.8 | 0.4 | 4 | 13.3 | 0.1 |
| Mastoid breadth | 11.3 | 12.1 | 4 | 11.1 | 0.1 | 13 | 11.5 | 0.1 | 4 | 11.3 | 0.2 |
| Inteorb. constrict. | 4.0 | 4.4 | 4 | 4.4 | 0.2 | 13 | 4.3 | 0.1 | 4 | 4.2 | 0.1 |
| Nasal length | 8.4 | 10.3 | 4 | 7.8 | 0.7 | 13 | 8.7 | 0.4 | 4 | 9.6 | 0.2 |
| Frontal length | 9.1 | 9.7 | 4 | 9.1 | 0.2 | 13 | 9.0 | 0.3 | 4 | 9.4 | 0.5 |
| Parietal length | 5.1 | 6.4 | 4 | 4.4 | 0.2 | 13 | 5.0 | 0.4 | 4 | 5.2 | 0.2 |
| Incisor foramina | 5.5 | 6.4 | 4 | 5.3 | 0.3 | 13 | 5.6 | 0.3 | 4 | 6.1 | 0.3 |
| M1M3 alveolar | 3.5 | 4.3 | 4 | 4.0 | 0.1 | 12 | 4.1 | 0.2 | 4 | 4.4 | 0.1 |
| m1m3 alveolar | 3.8 | 4.5 | 4 | 4.1 | 0.1 | 13 | 4.2 | 0.2 |  | 4.5 | 0.3 |

## Chromosomal analysis

35 specimens of $A$. iniscatus have a chromosome complement of $2 \mathrm{n}=34, \mathrm{FN}=42$ (Fig. 3). These include 29 specimens from the Puerto Madryn area, 2 from Punta Lomas, and 4 from Collón Curá. Specimens from all three localities show the same karyotype. The first four pairs are large biarmed chromosomes distinguished from the remaining autosomes by a sharp size gap. Pair 1 is submetacentric, whereas pairs 2 to 4 are metacentric. Pairs 5 to 15 are telocentric. As in most akodontines, the last autosomal pair, (16), is a small metacentric. Pair 5 is medium-sized and pairs 6 to 16 are small autosomes gradually decreasing in size. The X and Y are small telocentrics, representing $5.12 \%$ and $2.46 \%$ of the complement respectively.

A male and a female from Puerto Madryn, which presented a heteromorphic Robertsonian variant of $2 n=33, F N=42$ were found. The decrease of $2 n=34$ to 33 results from the presence of a metacentric chromosome whose G-band pattern matches the combined banding patterns of telocentric autosomes 9 and 11 of the $2 \mathrm{n}=34$ karyotype (Fig. 3D).

C and G banding results refer only to the Puerto Madryn sample. Well-developed pericentromeric C-bands (Fig. 3B) are present on nearly all autosomes of A. iniscatus, in striking contrast to other species of the genus, which are usually C poor. Additionally pair 16 shows a band in the telomeric region of both arms, and pair 5 shows a small interstitial band. G-bands are illustrated in Fig. 3C.
A. puer has a karyotype of $2 \mathrm{n}=34, \mathrm{FN}=40$ (Fig. 3). The first three pairs are large biarmed chromosomes, differing sharply from the remaining autosomes in size. Pair 1 is submetacentric and pairs 2 and 3 are metacentric. Pair 4 is medium-sized telocentric, and pairs 5 to 15 are small telocentrics. Pair 16 is a small metacentric one. The X chromosome is a medium-sized $(6.87 \%)$ subtelocentric and the Y is a small $(2.20 \%)$ telocentric chromosome.

C-bands (Fig. 3B) show that heterochromatin is found only in the short arm of the X and in the centromeric region of the Y. G-bands of A. puer are presented in Fig. 3C.

Fig. 4 shows the G-band correspondence between $A$. puer and $A$. iniscatus. This comparison reveals that 38 arms are shared by both species. Of the 38 shared arms, 28 belong to 24 whole chromosomes, two of which are biarmed. The remaining 10 shared


Fig. 3. Akodon puer and A. iniscatus giemsa stained karyotypes (A), C-bands (B), and G-bands (C). A. iniscatus heteromorphic pair of $2 \mathrm{n}=33$ morph (D)


[^0]arms do not correspond to whole chromosomes in both species. Pair 9 of A. iniscatus and the short arm of the X of $A$. puer are unique elements to these species. Low G-band resolution of pair 16 did not clarify if this pair is shared between both species. Since the microchromosomal pair is present in most Akodon species, we conventionally take it as a shared pair. Although, the size difference between pair 16 of A. iniscatus and A. puer suggests an addition of heterochromatin in the former.

In order to analyze the shared chromosomes between both species we nominate $A$. puer as " $A I$ " and $A$. iniscatus as " $A I$ "; short arm as " p " and long arm as " q ". Arm 1 q and pairs 2 and 3 are shared by both species. The 1 p of $A P$ is shared with the 4 p of $A I$. Chromosome 4 of $A P$ is shared with 4 q of $A I$. Chromosome 9 of $A P$ is shared with 1 p of $A I$. Pairs 5, 6, 7, $8,10,11,12,13,14$, and 15 are shared by both species. Thus, two biarmed autosomes of both species can be postulated as shared chromosomes. The remaining biarmed chromosomes (pairs 1 of both species and pair 4 of $A I$ ) result from Robertsonian rearrangements of different arms showing monobrachial homology (Fig. 4C) (BAKER and Bickham 1986; Capanna et al. 1985; Corti et al. 1986).

Fluorescent bands are illustrated in Fig. 5. In the $A$. iniscatus karyotype (Fig. 5C), most CMA-positive bands occur within the euchromatin and in the telomeric heterochromatic region of pair 16. The remaining heterochromatic regions are CMA-negative. All CMApositive bands seem to correspond with G-negative bands, with the exception of pair 16. Fluorescent CMA-bands suggest heterochromatin similarity in base composition among centromeric regions, as well as heterochromatin heterogeneity between these regions and the telomeric region of pair 16. A. iniscatus Q-bands (Fig. 5D) show that fluorescent and quenched Q-bands seem to correspond with G-positive and G-negative bands respectively, although better banding resolution is found in G -bands. The Q banding pattern is opposite to that obtained with Chromomycin $\mathrm{A}_{3}$, except in the centromeric regions that are CMA-negative and Q-negative. A. puer CMA-bands (Fig. 5A) reveal that CMApositive bands are located within the euchromatin, in regions which were identified as Gnegative.

Heterochromatin observed in the sex chromosomes is CMA-negative. A. puer Q -bands (Fig. 5B) show that the Q-band pattern, as in A. iniscatus, is opposite to that with Chromomycin $\mathrm{A}_{3}$. The same correspondence between Q and G bands as in $A$. iniscatus was found.

## Discussion

Several results indicate that akodontine rodents underwent an intensive chromosomal evolution. The high degree of cladogenesis exhibited by 11 genera and 66 species belonging to the tribe (Reig 1987), is correlated with a high number of chromosomal rearrangements. However, this correlation does not imply an overall causal link between evolutionary divergence and chromosomal changes in the Akodontini. Within Akodon, a high range of chromosomal numbers is found, from $2 \mathrm{n}=14$ in A. arviculoides (Yonenaga 1972) to $2 \mathrm{n}=$ 52 in A. illuteus (Liascovich et. al., 1989), A. longipilis (Spotorno and Fernandez 1976), A. olivaceus (Gallardo 1982), etc. Species of the genus Akodon can be divided into two assemblages according to their overall karyotype characteristics. Species of the first group have a varying karyotype of around $2 \mathrm{n}=40$ chromosomes which may be reduced by fusions, the second group comprises species with a uniform $2 n=52, F N=56$ karyotype. A good knowledge of the degree of whole chromosome and arm sharing among the species is required for this study.

The term "shared chromosomes" refers to whole chromosomes or chromosome arms which share banding patterns. G-banding was first employed to analyze chromosomal homology of akodontines in a study of $A$. azarae, A. molinae, and " $A$." obscurus (BiANCHI et al. 1976). Full chromosome arm homology of species sharing the $2 \mathrm{n}=52$ karyotype was
demonstrated in A. longipilis, A. olivaceus and A. sanborni (Gallardo 1982), A. xanthorbinus (Rodriguez et al. 1983), and A. illutens (Liascovich et al. 1989). Bianchi and Merani (1984) studied the karyological relationships among several akodontine species of the varying karyotype group: A. azarae, A. dolores, A. molinae, A. mollis, "A." obscurus,


Fig. 5. Fluorescent banded karyotypes. A. puer CMA-bands (A), and Q-bands (BB); A. iniscatus CMA-bands (C), and Q-bands (D)
A. urichi, and $A$. varius. They demonstrated a high degree of arm sharing among species, which had mostly diverged by presumed Robertsonian processes. These studies are germane to the hypothesis suggested by Bianchi et al. (1971) that chromosome evolution within the akodontine rodents proceeds from low to high numbers by centromeric dissociations, or conversely from high to low numbers by centromeric fusions. One of the present authors (Reig 1987; Vitullo et al. 1986) claimed that the second alternative is the most plausible. Our present results show a high degree of chromosomal homology between $A$. iniscatus and $A$. puer, which suggests close phylogenetic relations between these species. The reductional process of chromosomal number in these two species involved metacentrics, resulting from the fusion of the same autosomes, and then give fully shared chromosomes, and of metacentrics derived from the fusion of different telocentrics which show merely monobrachial homology. Baker and Bickman (1986), Capanna et al. (1985), Corti et al. (1986), and Moritz (1986), have recently pointed out that monobrachial homology probably results in full hybrid sterility. The degree of meiotic breakdown depends on the number of fusions that are monobrachially homologous, and on the specific chromosomes involved. Generally, those studies are based on hybrids with monobrachial homology. The allopatric distribution presented by the species under study led us unable to find hybrids in nature. In order to evaluate the extent of monobrachial homology as a cause of hybrid sterility, studies on laboratory hybrids should be done.

The finding of a polymorphism for one Robertsonian rearrangement in two of the thirty seven studied specimens of $A$. iniscatus is in good keeping with the general occurrence of Robertsonian translocations in the group. In the Puerto Madryn population, this fusion polymorphism is not as extensive as it is in A. dolores, A. molinae (BiAnCHi and Merani 1980), and $A$. simulator (Liascovich et al. 1989). In view of the extensive arm homology found between $A$. iniscatus and $A$. puer, it was of interest to investigate if other chromosomal changes revealed by more refined techniques were involved in the differentiation of these related species.

As species of Akodon usually show very little heterochromatin, it was unusual to find a wide-spread occurrence of centromeric heterochromatin in the $A$. iniscatus complement. The few previously known cases of centromeric heterochromatin in Akodon were in A. mollis (Lobato et al. 1982), A. arviculoides, A. aff. arviculoides (Yonenaga et al. 1975; Yonenaga-Yassuda 1979; but see Honacki et al. 1982, and Liascovich and Reig 1989, for correct naming of these forms), $A$. (Deltamys) kempi (Sbalqueiro et al. 1984), and $A$. (Hypsimys) budini (Vitullo et al. 1986), in which modest amounts of heterochromatin have been described. Relevant to our study is the fact that C-positive bands are almost nonexistent in $A$. puer and $A$. azarae (Vitullo et al. 1986), both of which are considered to be closely related to $A$. iniscatus (Reig 1987).

In other groups of mammals, G-banding patterns appear to be quite stable, but extensive interspecific variation in constitutive heterochromatin has been reported (Arnason 1974; Elder and Lee 1985; Pathak et al. 1973; Stock 1981). We have no indication of the processes which were involved in the presence of the centromeric and telomeric heterochromatin, or of its function in $A$. iniscatus, but it is relevant to these problems to have found sequence diversity in the heterochromatin of $A$. iniscatus.

Some fluorescent antibiotic dyes exhibit a nucleotide specificity with helical DNA. A guanine and cytosine (GC) specificity was found for chromomycin $A_{3}$ (Sahar and Latt 1978, 1980), whereas a less clear adenine and thymine (AT) specificity has been proposed for quinacrine (Comings 1978). Despite the fact that the molecular mechanisms of interaction between these specific fluorescent dyes and DNA are not well known, they permit a cytological characterization of presumed heterogeneity of DNA sequences within the genome (Barros and Patton 1985).

Chromomycin $A_{3}$ has revealed heterogeneity between the heterochromatin of all chromosome pairs and the telomeric heterochromatin found in pair 16 of $A$. iniscatus
karyotype. The latter type of heterochromatin appears as predominantly GC rich, whereas the former is not. This telomeric heterochromatic region is not observed in A.puer's pair 16. An increase/decrease of this GC rich region could be responsible for the size difference observed in pair 16 between the species analyzed.

John et al. (1985) present a review of the concept of equilocality, the similar location of C-bands found between non-homologous chromosomes within the complement. By comparative fluorescence studies on heterochromatin of acridid grasshoppers, these authors found that certain groups of chromosomes that presented a similar C-band distribution also showed a similar fluorescence behaviour with specific dyes, although heterochromatin heterogeneity was also found between similar sites which differ in size and structure. A form of equilocality is present in A. iniscatus where all chromosomes, except pair 16, carry a C-band at a centric location, which is CMA and Q negative, while a different heterochromatic site (telomeres of pair 16) respond differentially to CMA.

Although centromeric regions in $A$. iniscatus are heterochromatic, while those in $A$. puer are euchromatic, no fluorescent staining difference was found between them. Findings of CMA and Q negative fluorescence in centromeric heterochromatin could reflect an insufficient number of AT or GC clusters of DNA (Schweizer 1981; Sahar and Latt 1980). While DNA composition is an important determinant in fluorescence staining, the possible role of chromosomal proteins remains unknown (Comings 1978). Comparison of the centromeric regions of $A$. iniscatus and $A$. puer therefore needs to be defined by further sequence analysis. Coincidentally, no composition differences were found between the remaining complement of both species, except for pair 16, which also confirms the chromosome correspondence analysis based on G-bands.

In biarmed complements, equilocality has been explained in terms of a specific ordering of the chromosomes during metaphase (Schweizer and Ehrendorfer 1983), where a sequence transposition or convergence is assumed to occur between repeated sequences of chromosomes in proximity, but according to Joнn et al. (1985) the initial production of Cbands could occur by sequence amplification. Although we don't know if a non-random chromosome distribution is present in A. iniscatus, chromosome interactions between centromeric heterochromatic areas have been found to occur between several chromosomes at metaphase (Fig. 6). Following Jонn et al. (1985), an alternative basis for equilocal distribution of centric heterochromatin in $A$. iniscatus could be explained by concerted amplification of the centromeric C -bands between non-homologous chromosomes.

A peculiar result of this study is the finding of a reduced $2 \mathrm{n}=34$ karyotype of the varying $2 \mathrm{n}=40$ chromosome group in $A$. iniscatus, as this species inhabits an area where all the remaining akodontine mice show the constant $2 \mathrm{n}=52$ karyotype. The latter was found in A. andinus, A. brachiotis, A. hershkovitzi, A. illuteus, A. longipilis, A. olivaceus, A. sanborni, A. xanthorbinus, and in species of Geoxus and Chelemys (but see Reig 1987, and Liascovich et al. 1989), all of which inhabit the southern Andes and the Patagonian tableland. Reig $(1984,1986,1987)$ recently postulated that the akodontine radiation took its origin in the Puna region during Miocene times from a $2 \mathrm{n}=52 \mathrm{~A}$. andinus-like Akodon ancestor. From this area of original differentiation a chromosomally conservative phylad dispersed to the southern Andes and to Patagonia, maintaining the original $2 \mathrm{n}=52$ karyotype unaltered in a cladogenetic process which involved species of the subgenera Akodon and Abrothrix and genera such as Chelemys, Geoxus, and Notiomys. Another main dispersing branch descended from the Puna to the southeastern lowlands, presumably from a $2 \mathrm{n}=40 \mathrm{~A}$. boliviensis-like species, giving rise to the different species in central and northern Argentina, Paraguay, Brazil, and Uruguay. Regarding the origin of $A$. iniscatus and the related (and now considered co-specific) Neuquenian form A. nucus. Two alternative hypothesis were postulated by ReIG (1987): both forms may have derived from the southern Andean branch or from the southeastern lowland one. Reig inclined himself


Fig. 6. Chromosome interactions between centromeric heterochromatin in A. iniscatus
toward the second alternative in view of the greater morphological similarities of these forms with $A$. puer and $A$. azarae. The results presented here indicating a high chromosomal similarity between $A$. iniscatus and $A$. puer are consistent with the latter hypothesis.

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## Resumen

Comparación de patrones de bandeo entre Akodon iniscatus y Akodon puer (Rodentia, Cricetidae)
Se describen los cromosomas de Akodon iniscatus ( $2 \mathrm{n}=33-34, \mathrm{NF}=42$ ) y se comparan con el cariotipo de A. puer ( $2 \mathrm{n}=34, \mathrm{NF}=40$ ). Se estudian los patrones de bandeo C , G y fluorescentes ( Q y CMA) de 37 ejemplares de $A$. iniscatus y 11 de $A$. puer. A. iniscatus presenta heterocromatina localizada principalmente en la región centromérica, la cual está ausente en A.puer y es poco frecuente en otros akodontinos. Las bandas de cromomicina revelan que la heterocromatina de la región centromérica de todos los cromosomas es homogénea y pobre en GC, mientras que la heterocromatina telomérica es rica en GC. Ambas especies comparten brazos cromosómicos y cromosomas completos, siendo 38 los brazos en los que se encuentra el mismo patrón de bandas G. Estos resultados apoyan la hipótesis de una cercana relación entre $A$. iniscatus y $A$. puer y sugieren que la primera probablemente deriva de un stock akodontino que originalmente se diferenció en las tierras bajas del noreste de Argentina. Por lo tanto, A. iniscatus estaría relacionada con el grupo de especies de Akodon de alrededor de 40 cromosomas.

## Zusammenfassung

Vergleiche von Bandenmustern zwischen Akodon iniscatus und Akodon puer (Rodentia, Cricetidae)
Der Karyotyp von Akodon iniscatus $(2 \mathrm{n}=33-34, \mathrm{FN}=42)$ wird erstmals beschrieben und mit dem von $A$. puer $(2 n=34, F N=40)$ verglichen. Dazu wurden die C-, G- und Fluoreszenzbandenmuster
(Q, CMA) von 37 A. iniscatus und 11 A. puer untersucht. Eine Reihe ganzer Chromosomen und 38 Chromosomenarme besitzen bei beiden Arten gleiche G-Bandenmuster. Im Gegensatz zu A. puer und den meisten Akodon-Arten besitzt A. iniscatus auffälliges Heterochromatin in der ZentromerenRegion. Die CMA-Färbung zeigt, daß das Heterochromatin der Zentromeren-Region arm an den Basen CG ist, wogegen das telomerische Heterochromatin deren viele enthält. Der Vergleich der Chromosomen spricht insgesamt für eine enge Verwandtschaft von A. iniscatus und A. puer. A. iniscatus hat sich wahrscheinlich in tiefgelegenen Gebieten im Nordwesten Argentiniens differenziert und ist innerhalb von Akodon der Artengruppe mit etwa 40 Chromosomen zuzuordnen.

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Authors addresses: Maria A. Barros, Rosa C. Liascovich, Osvaldo A. Reig, Gibe, Dpto. de Cs. Biológicas, FCEyN, Universidad de Buenos Aires, Pabellón 2, 4to. piso, Ciudad Universitaria, Núñez, 1428 Buenos Aires, Argentina; Luz Gonzalez, Instituto de Evolución y Ecologia, Universidad Austral de Chile, Valdivia, Chile; Martha S. Lizarralde, Centro Austral de Investigaciones Científicas, CONICET, Ushuaia, Argentina


[^0]:    Fig. 4. G-banding pattern comparison between $A$. puer (left) and $A$. iniscatus (right). Pair numbers correspond to their position in each species' karyotype (A).
     (C)

